

8.

The Function of Secondary Sexual Characters
in Two Species of Dynastidae (Coleoptera).¹

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(PLATES I-V).

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These notes have to do with two species of dynastids, *Megasoma elephas* Fabr., 1775, and *Strategus aloeus* Linnaeus, 1758. The Venezuelan name for these beetles is *Tornado*, the borer. Another name is *Congaroch*, and in the Andes they are known as *Bobute*.

These so-called elephant beetles were observed and collected at Caripito, north-eastern Venezuela, in the course of the Forty-third Expedition of the Department of Tropical Research of the New York Zoological Society, during a period of seven months, from February to September, 1942. The photographs, both stills and motion-pictures, were taken by Miss Jocelyn Crane, Research Zoologist on the staff of the department.

Only once did I find the big *Megasoma* and the smaller *Strategus* under normal conditions. On March 18 a female of the latter was observed crawling up the trunk of a small jungle tree, and a few days later two male *elephas* were discovered resting beneath an overhanging branch, on a half-rotten log, quite hidden from view.

On March 20 I found a female *Strategus* in a spider web of unusual strength and size, the large rufous-bodied owner frantically wrapping up the struggling beetle. On the

same day, a half-mile away, a member of my staff came across an identical occurrence, only here the victim was a male. All others of both species were taken when flying at night against the screened windows of the laboratory, or around the electric lights in the compound, or on the ground on their backs, in early morning, within the radius of the same lights. Their appearance, however, was only during or after a rain. Fewer than fifty of each species were taken during our whole stay. In *Megasoma* the sexes seemed about equal, but *Strategus* females dominated almost six to one. From the beginning of the rains on April 27, both species became more abundant, several often being taken close together in the mornings beneath the lights of the refinery. None were seen after July 12.

The great development of horns of varying sizes and shapes on the head and thorax of male beetles of the family Dynastidae has long attracted attention and excited speculation. These specialized structures in connection with the great size of the beetles are reflected in many technical names: *Dynastes*, *Megasoma*, *Megaceros*, *Goliathus*, *elephas*, *hercules*, *rhinoceros*, *atlas*, etc.

Charles Darwin in 1871, in the first edition of "The Descent of Man," (Vol. I, pp. 371-372) wrote as follows:

"The extraordinary size of the horns, and their widely different structure in closely-allied forms, indicate that they have been formed for some important purpose; but their excessive variability in the males of the same species leads to the inference that this purpose cannot be of a definite nature. The horns do not show marks of friction, as if used for ordinary work. Some authors suppose that as the males wander much more than the females, they require horns as a defence against their enemies; but in many cases the horns do not seem well adapted for defence, as they are not sharp. The most obvious conjecture is that they are used by the males for fighting together;

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but they have never been observed to fight; nor could Mr. Bates, after a careful examination of numerous species, find any sufficient evidence in their mutilated or broken condition of their having been thus used . . . The conclusion, which best agrees with the fact of the horns having been so immensely yet not fixedly developed,—as shown by their extreme variability in the same species and by their extreme diversity in closely-allied species—is that they have been acquired as ornaments. This view will at first appear extremely improbable; but we shall hereafter find with many animals, standing much higher in the scale, namely fishes, amphibians, reptiles and birds, that various kinds of crests, knobs and horns have been developed apparently for this sole purpose.”

Eight years later, Alfred Russel Wallace in “Tropical Nature” (p. 372) writes of the “immense horns of some beetles of the families Copridae and Dynastidae, which Mr. Darwin admits are not used for fighting, and therefore concludes are ornaments, developed through selection of the large-horned males by the females. But it has been overlooked that these horns may be protective. The males probably fly about most, as is usually the case with male insects; and as they generally fly at dusk they are subject to the attacks of large-mouthed goatsuckers and podargi, as well as insect-eating owls. Now the long, pointed or forked horns, often divergent, or movable with the head, would render it very difficult for these birds to swallow such insects, and would therefore be an efficient protection, just as are the hooked spines of some stingless ants and the excessively hard integuments of many beetles, against the smaller insectivorous birds.”

Passing by some other comfortingly easy explanations we come to the antithesis, given for what it is worth at third hand in “A Year of Costa Rican Natural History” by A. S. and P. P. Calvert (1917). The authors write (p. 69), “Dr. Ohaus has also kindly informed us that a correspondent of his friend Herr Nagel has observed, in Venezuela, that the males of *Dynastes hercules* fight very violent battles among each other for the females; that they seize and crush with the cephalic and prothoracic horns, the weaker male often having its thorax and elytra crushed, and that the victorious males take the females between the horns and carry them away.” This anonymous information coming to us through three subsequent channels requires, I think, considerable confirmation, especially as to the direct crushing power of the horns and the ultimate use of these structures in the Sabine-like kidnapping of the female.

In these and numerous other contributions we have a number of suggestions as to the use of these horns: ornaments, direct

defence against attacks from enemies, and indirect in making ingestion by large-mouthed assailants difficult or impossible, transportation of the female, overdevelopment as sheer, useless impetus of secondary sexual characters, scraping and puncturing bark to induce the flow of edible sap, and fighting among themselves for the possession of the female.

Although I have often kept these giant beetles in vivaria in the tropics, I have never seen, either in free or captive specimens, any confirmation of any of these suggested uses of the horns until April 13, 1942, in the Zoological Society’s laboratory at Caripito, northeastern Venezuela.

For a fortnight I had kept three males and a female *Megasoma elephas* in a glass battery jar. The quartet of big beetles had fed steadily on over-ripe banana, their method of feeding being to push and nuzzle into the soft pulp until they were quite plastered with the fruit. In a general cleaning of laboratory cages on this 13th of April I carried the jar and its contents to an outside faucet and held one beetle after another beneath the swift stream of water. When picked up, as usual they turned and twisted, the tearing power of their sharp claws and the pinching strength of head armor against the edge of the thorax making it difficult and painful to hold them. During the process of washing they became quiet and did not move a leg again until returned to their cleansed cage.

I returned the jar to its place, gave the beetles a supply of fresh banana and forgot them until a half-hour later when I heard a confused sound. I found the food neglected and the three males in an intricate pile, massed around the female. I removed her and from this moment on the battling of the males among themselves occupied considerable of our attention. Food was completely ignored in the newly aroused heat of battle. When from exhaustion or other cause the combative instinct died down, I could always initiate new and violent encounters by either an application of the water treatment, or the introduction of a female. Two or three days of enforced drought would reduce the war to casual skirmishes, ineffectual feints, and a renewed interest in the mushy fruit. It seemed more than a coincidence that on April 27, only fourteen days after the transformation wrought by the artificial deluge of the water faucet, the actual rainy season began. In my precocious breaking of the dry season I had anticipated the effect of the annual rains in unlocking the reproductive reactions of these great insects.

Concomitant with this suddenly aroused combativeness was nocturnal activity. From now on we were constantly disturbed by loud drummings and reverberations from the beetles, and found that from dark to

midnight both males and females sought to escape from their cages by flight. The loud banging was due to the impact of the spread elytra against glass and wire, driven by the powerful vibration of the flight wings. This activity ended about twelve or one o'clock and for the rest of the night the beetles rested quietly or fed.

MATING OF *Megasoma elephas*: After being drenched with water a pair of beetles would mate almost immediately, whether after long confinement together during which their chief interest was in the banana fodder, or whether both insects had been just caught and placed together. There was no hint of preliminary courtship, no opportunity for appraisal of the horns as ornaments by the female or sexual selection. If no rival was present, the male went straight for the relatively small female and when within reach hauled her toward him, and mating took place at once.

When the male first mounts he wraps his fore legs around the female, sliding them into the lateral crevice between the armor of her head and thorax. In this grip he makes no use of tarsi and terminal claws, but only of the stout, spiny tibia. The second pair of legs hook underneath her body on to the bases of her legs, the terminal claws functioning in this case. When copulation is attained his position changes radically. He now rears almost straight upright, his whole body becoming vertical, resting on his rear tarsi, with the front pair of legs and often the second dangling in the air above the back of the female.

This identical procedure was followed in the first three matings and in a fifth. In the fourth, between a newly caught female and the same male in mating number two, the finale was slightly varied. While the male was in quite as vertical a position, he had shifted the hold of his fore legs, which now clung by the terminal claws of the tarsi to the basal joints of the forelegs of the female, while both second and third pairs of legs dangled free in mid-air. This resulted in a triangular support; his juncture with the female plus the backward pull with his forelegs.

After the water treatment, even if a male was half-immersed in a banana, if a female was dropped into the cage, he instantly became aware of her and rushed in her direction. If a male was substituted the feeding male made no mistake, but, slimy banana and all, went for the new-comer and engaged him head on. In nervousness and quickness his reactions speeded up one hundred per cent. His ordinary activity is a heavy crawling, a slow, bungling creeping with the body dragging. When preparing to mate or fight the body is raised clear and the movements are quick and dynamically directed. In the preliminaries of both

activities there is often a series of rhythmic jerks.

EGGS: On May 23 we noticed in the cage which contained five *Megasoma* females that the detritus was in the form of small, rounded balls of dark-colored material, although there was nothing in the enclosure but sections of over-ripe banana. In two cages containing males the excreta was nothing but formless masses of food. I dissolved several of the balls but found no trace of eggs. On May 25, however, Miss Crane discovered the first egg lying loose on the bottom, and after this several appeared every day, but with no relation to the rounded masses of material. Decayed logs put in with the females aroused no interest whatsoever. The eggs measured 4 by 4.7 mm., the surface being smooth, and ivory white.

FIGHTING OF *Megasoma elephas*: Although the battle between each individual pair of male beetles is, to a certain extent, slightly different from every other, yet there are several fundamental phases which seem invariable. The opponents meet head on, and either warily wait for the other to attack, or one may rush headlong and begin the encounter. Usually both wait and spar at a little distance. The object first noticeable is an attempt with one or both fore tarsi and claws to trip and unbalance the opponent. This is evident in a long series of single photographs and in several complete kodachrome motion picture sequences. There are quick forward lunges and reachings out with one or both legs, sometimes at the same moment by both insects. This may or may not succeed, but one will force the fighting and the result may be straight pushing and butting for a considerable period, exactly like two antlered deer. Now and then an effort will be noticed to lower the head and get the cephalic horn beneath the other insect. Again and again this is tried, and both may attempt it at the same moment. Then recur the rearing and tripping attempts.

Periods of rest or waiting may intersperse the encounter and twice I have seen one beetle turn and rush after the female. In both cases the other was after him full speed and the battle began again. The female never remained, but went off as far as the confines of the cage, or in the case of the fight taking place in the open, as far as we would allow her to go, when we would recapture her for fear of losing her in the underbrush. The only certainty was that she showed not the remotest interest in the encounter or in either of her suitors. In all our experience with these beetles, which was invariably in the daytime, we never saw either sex take to wing.

Unexpected phases often interrupt the regular succession of the happenings I have

mentioned. The pull of the sharp, curved claws often unbalances both beetles at once and they lose their footing and roll over and over, all twelve legs tangled together and entailing considerable awkward effort before they separate and face each other again. It is astonishing how loud the clash of horn against horn becomes when one's ear is close to the fighters. The insects are usually horizontal when they begin pushing against each other, but attempts at tripping will cause both to rear up high on the second and third pairs of legs. Then, if at all, comes the final phase, the all out attempt to get the tip of the curved bifurcated horn caught in the soft skin of the ventral joint between the thorax and abdomen. Once secured, we realize this is evidently the chief object of the encounter. The successful one puts forth all the strength of which he is capable and lifts again and again with all his might. The higher the other is lifted the more helpless he becomes as his feet, one after the other, leave the ground, and with several super-beetle flings the victim of this grip is thrown over on to his back. Not once, but again and again this was the end result. Often the beetle simply rolled over and came back on his feet again and the whole engagement recommenced, but sometimes he landed on his back and if the surface was at all level and smooth, he spun helplessly waving all six feet in mid-air. The winner began searching in all directions, evidently for the female. Yet if replaced by himself in a cage he soon settled down to immobility.

The whole encounter was reminiscent of the broomstick or cane encounters of our childhood's parties, where the hands of two boys were tied and a cane inserted behind knees and above elbows and the ensuing encounter was, by manipulation of the ends of the stick or otherwise, to roll the opponent over on his back, when he became as helpless as an upset beetle.

The Middleweight Elephant Beetles (*Strategus aloeus*) fought as readily as their larger relations and in almost exactly the same manner. An important difference between the two species is that *Strategus* has all three horns on the thorax, while *Megasoma* has the central curved horn on the head itself. Although thus denied the inter-mobility of the horns, the smaller beetles fought with equal fury and quite as satisfactory results. The general plan of battle was identical, to get the anterior horn beneath their opponent and lever him up and over. In one of the first fights watched there were several momentary lockings and once the attacker was himself pried into the air and almost on his back. When upside down this species seemed even more helpless

than the larger, and I believe would die of starvation on a smooth surface if left to themselves. The general movement and activity was less evident owing to the lack of separate play of horn number one, but there was no lack of fierce effort.

These accounts have been general ones. The following are notes which I took on two individual encounters:

On April 13 two *Megasoma* males after showing desire for battle were placed by themselves in a large open space and they instantly began fighting. They were the two largest of the three which had been kept together for two previous weeks and during that time had, as I have said, shown no great interest in each other or the female, concentrating solely on resting and feeding. This fight was short. The two rushed together and the horns met with a distinct click. For three minutes they pushed, bracing their feet with all possible power. Then separating they did it all over again. The larger one of the two seemed to have the advantage and after three attempts inserted his horn beneath the body of his adversary and actually tossed him clear of himself and the ground. In this case he was on top of the beetle before he could right himself or attempt to do so, and in the ensuing maze of waving legs, the successful male was almost overcome. Again he upset the smaller and again he foolishly helped him to his feet by rushing upon him. At the third and last upset I distinctly saw the horn of the larger beetle push and tear the membrane of the ventral joint, and examination confirmed this damage, slight though it was. A stalemate of pushing ensuing, I separated them for the night.

Disparity in size both between individual males and also sexually is very marked in *Megasoma*. An average male weighs 32 grams and a female 24 grams. The males vary between weights of 28 grams and 36 grams, with corresponding total lengths of 85 mm. and 103 mm. When a number of males are compared they seem to fall into two general nodes to which we gave the names of Major and Minor.

For several days a female and a minor male had been confined together and they had mated. I introduced a major male on May 21, and after righting himself he clambered awkwardly over the small male and toward the female. His antennae played over her back for a few seconds and then the lesser male blundered past him. Like a flash the major turned on the other beetle and the fiercest fight we had seen thus far was on. Both of course tried to get the curved horn under the other, both tried to trip the other off balance. Three times Minor was actually tossed into the air and landed on his back. He levered himself upright and

after the third event he seemed to become thoroughly aroused and fought twice as hard as before. His very smallness of size was a help in some ways and the locked horn gave the larger insect little advantage. Once the giant was turned over and fell on the female and instantly the minor rushed at both and while they were tangled, butted and drove against them and rolled them about. The larger finally got his opponent in a corner and hooked and twisted violently, securing some strange, secure lock and after a wrench we saw the right middle leg of the smaller beetle break off near its base and lie kicking by itself on the ground. Not for a moment did the injured beetle stop his efforts, but I now retrieved him. The same five-legged minor on the following day mated without trouble with two freshly caught females.

After removing the wounded beetle I substituted another major and the combat went on. Both beetles met head on and for at least three minutes, pushing and twisting and jerking with all their might, neither could apparently break the lock. It was like two deer whose antlers have sprung together beyond all possibility of breaking apart. I separated the beetles and found that the apparent locking was due only to uninterrupted pushing, and that in reality the two beetles were quite free to move apart whenever one of them should relax his efforts.

As I said earlier, I neither anticipated nor saw any attempt at carrying the female, and in fact we were unable to push the

large-bodied female between the three horns even temporarily, so that such an improbable feat, as reported in *Dynastes hercules*, seems impossible in the present species.

Even at the height of violent combative activity, I saw no possibility, either in their encounters or in my handling, of any sufficient direct force strong enough to crush or fracture the extremely hard body or elytral armor. The only injuries observed were the slight tearing of the intra thoracic and abdominal ventral membrane, and the snapping of a leg by oblique leverage.

The succession of still photographs of live, unposed beetles taken in two-hundredths of a second presents fairly satisfactory visual realization of this phase of activity of these giant beetles. Proper appreciation of the quickness of movement, the un-scarab swiftness and deftness of use of legs and horns can only be had from the kodachrome motion pictures of the entire conflicts.

SUMMARY: Male beetles of two species of Dynastidae, *Megasoma elephas* and *Strategus aloeus*, use their cephalic and thoracic horns for fighting with each other.

The initial stimulus is the beginning of the rainy season. Nocturnal and mating activity are consequent upon individual rains. In captivity both can be aroused to highest pitch and culmination by artificial applications of water.

The phases or methods in fighting in both species are identical, first an attempt to unbalance the opponent by tripping, and then by ventral attack with the anterior horn to lift and throw him upon his back.

EXPLANATION OF THE PLATES.

These fourteen photographs supplement the verbal portion of this paper, and take the place of the kodachrome motion picture sequences which are limited to a screen. The individual beetles are the same throughout, but three photographs have been interpolated from second and third encounters between the same contestants. These fourteen are selected from a total of sixty-nine. All were taken by Miss Jocelyn Crane.

The battle took place in the compound of the laboratory at Caripito, Venezuela. *Photographic data:* camera, Leica; lens, Leitz 90-mm. Elmar; film, Eastman Super-XX. Figs. 1-7 were made by sunlight alone, exposure 1/60 sec., f:12.5; figs. 8-14 by synchroflash, exposure 1/200 sec., f:16.

A male elephant beetle, *Megasoma elephas* approaches a female (Figs. 1 and 2). While

he prepares to mate, a second male approaches (Figs. 3 and 4). The new arrival attacks (Fig. 5) and separates the mating pair (Fig. 6). The beetles meet head on (Fig. 7) and in their efforts to trip each other, rise on their second and third pairs of legs (Fig. 8). As frequently happens, the tripping is mutually successful and both are upset (Fig. 9). They separate at once. In the course of the continued battle the first male succeeds in getting his cephalic horn beneath the head of his opponent (Fig. 10), and exerting all his strength lifts again and again, raising the beetle clear off his feet (Figs. 11 and 12), and rolling or throwing him over (Fig. 13). With the interfering beetle helpless on his back, beetle number one begins his search for the female (Fig. 14).